February 23, 1888.

Mr. JOHN EVANS, D.C.L., Treasurer and Vice-President, in the Chair.

The Presents received were laid on the table, and thanks ordered for them.

The following Papers were read:—

I. "On the Relation between the Structure, Function, and Distribution of the Cranial Nerves. Preliminary Communication." By W. H. GASKELL, M.D., F.R.S. Received February 9, 1888.

In a previous paper* I have pointed out that the structure, distribution, and function of the spinal nerves, as well as the arrangement of their centres of origin in the spinal cord, all lead to the conclusion that these nerves are divisible into two parts; (1) a somatic part, supplying the external surface of the body and the muscles derived from the muscle plates, and (2) a splanchnic part, supplying the internal surfaces and organs and the muscles derived from the lateral plates of mesoblast.

I also pointed out that the cranial nerves were built up on a similar plan and arose from similar centres of origin to the spinal nerves; that they too were divisible into somatic and splanchnic groups of the same type as in the spinal nerves.

In that paper I dealt especially with efferent nerves, and pointed out that the somatic efferent nerves are non-ganglionated, and pass from the nerve cells of the anterior horn direct to the muscles derived from the muscle plates; on the other hand, the splanchnic efferent nerves are divisible into a ganglionated and a non-ganglionated group, of which the non-ganglionated motor nerves arise from a lateral group of nerve cells forming part of the lateral horn, which are continued cranialwards as the separate nuclei of such nerves as the facial, &c., and pass from the anterior root to the muscles derived from the lateral plates of mesoblast; while the ganglionated efferent nerves arise either from the cells of Clarke's column or from those of the lateral horn or from both, and pass to the so-called sympathetic

* 'Journ. of Physiol.,' vol. 7, p. 1.

ganglia to supply the muscles of the vascular system, alimentary canal, &c.

The whole argument in that paper was based upon the structure and distribution of the nerves of anterior roots, so that in speaking of the sympathetic ganglia as ganglia of a splanchnic root, all the evidence for vasomotor nerves, &c., went to show that these ganglia might be considered as belonging to anterior (efferent) roots rather than to posterior (afferent) roots.

Again Onodi's observations that such ganglia are offshoots from the spinal ganglia on the posterior root do not militate against the motor character of these ganglia, since in the lower animals and in the first two cervical nerves of the higher animals both anterior and posterior roots pass into the spinal ganglion, so that there is no difficulty in imagining that as the motor portion of the original spinal ganglion travelled away from its parent ganglion mass, the motor or efferent nerves would no longer pass into the spinal ganglion but would pass free from it, being connected only with the separated vagrant portions of the original ganglion, *i.e.*, with the sympathetic system.

There is in fact no evidence to show that the anterior and posterior roots are not truly efferent and afferent, and there is also no evidence to show that the afferent ganglia have travelled away from their original situation in the same way as the efferent ganglia. We may therefore consider the ganglia of the afferent spinal nerves, both somatic and splanchnic, as *stationary* in position, and as forming the root ganglia of the various nerves, while the ganglia of the efferent spinal nerves are *vagrant*, and form the so-called sympathetic system.

A complete segmental spinal nerve is then composed of (1) anterior root with vagrant ganglion; (2) posterior root with stationary ganglion.

The anterior root again is divisible into two parts; (1) a large-fibred medullated, and (2) a small-fibred medullated part, of which the latter only is in connexion with the ganglia of this root; the non-medullated fibres being these splanchnic ganglionated fibres which have lost their medullary sheath in one or other of the ganglia.

If the cranial nerves are built up on the same type as the spinal nerves, it follows that in them too we must have (1) an anterior root and (2) a posterior root, with a root ganglion stationary in position close to the exit of the nerves from the central nervous system into which both anterior and posterior roots may or may not pass; also the anterior root must consist of a small-fibred ganglionated portion and a large-fibred non-ganglionated portion, the ganglion on the anterior root being in all probability vagrant and not stationary.

In order to see how far the cranial nerves conform to the same type as the spinal nerves, I will consider their structure and distribution seriatim, leaving out of consideration for the present the olfactory, the optic, and also, for reasons to be mentioned, the auditory nerves.

Beginning then with the IIIrd or oculo-motor nerve, we are dealing with a nerve whose function at the present time is purely motor, a nerve therefore which is ordinarily spoken of as representing an anterior root; in this nerve we find indications of a large-fibred and a small-fibred part. Tracing up these fibres outwards to their destination it is seen that the large fibres pass off to supply the eye muscles supplied by this nerve, while most of the small fibres separate out from the large fibres and pass directly into the ganglion oculo-motorii. This ganglion, which is in the main formed by these small medullated fibres of the IIIrd nerve, *i.e.*, radix brevis, is increased in size by the addition of ganglion cells formed on the radix longa from the trigeminal, and others in connexion with sympathetic fibres; the fibres in the ganglion are all of small size, and the short ciliary nerves which arise from it have not a single large fibre among them. The nerve fibres of the short ciliary nerves are almost all medullated, and according to most observers (Bidder and Volkman) are more numerous than those entering the ganglion, so that in this case these small nerve fibres which are motor to the ciliary and splanchnic muscles do not lose their medullary sheath in their passage through the ganglion, a peculiarity which distinguishes them from the motor nerves of the vascular system, and is suggestive in connexion with the fact that these muscles though unstriped in structure are to a certain extent voluntary in action.

Also the nerve cells of this ganglion are distinctly of two kinds, most of them unipolar, of the same type as those of a spinal ganglion, the minority multipolar of the type of the so-called sympathetic ganglion cells: this also suggests that this difference in the type of nerve cell is associated with the presence or absence of a medullary sheath in the nerves issuing from the ganglion, and does not necessarily imply that these unipolar cells are connected with posterior root fibres, and that therefore, as has been supposed, this ganglion is the root ganglion of the oculo-motor nerve.

We see then clearly that the oculo-motor ganglion is the ganglion of these small-fibred efferent nerves of the IIIrd nerve.

The IIIrd nerve then conforms in its structure, and in the vagrant character of its motor ganglion, to the plan of a spinal nerve as far as its anterior root is concerned. Where then is its posterior root? If it conforms to the plan laid down, the ganglion on the posterior root, *i.e.*, its root ganglion, ought to be situated on the nerve near its exit from the central nervous system, and here, in fact, I have found it in the nerves of man and sheep. I have made a series of consecutive

sections through the rootlets of the IIIrd nerve of man, beginning from its exit out of the brain and passing peripheralwards, and have found that in the different rootlets a well-marked ganglion is formed in the same way as any spinal ganglion, with, however, one important difference; the nerve cells and groups of nerve cells have degenerated, but their place and position remain conspicuously marked out with characteristically arranged masses of peculiar neuroglia-like connective tissue substance. So striking is the resemblance to a spinal ganglion, that with a low power it is difficult at first sight to believe that it is not a section of a functional ganglion which is exposed to view.

These degenerated ganglia are limited to a definite portion of each nerve rootlet just as in a spinal ganglion; centralwards of the ganglion the degenerated tissue can be traced as a strand of the same peculiar neuroglia-like connective tissue into the brain; peripheralwards of the ganglion all trace of altered nerve tissue or ganglion cells has disappeared.

Here then we have what appears to me without doubt to be the phylogenetically degenerated posterior root and root ganglion of the IIIrd nerve; so that in its posterior root, and in the situation of its root ganglion, it conforms also to the plan of a complete spinal nerve.

In the IVth nerve I find the same structure, an anterior root composed of a large-fibred portion and a small small-fibred portion; the destiny of this latter, and its connexion with any vagrant motor ganglion, I have not yet had time to trace out.

Soon after the IVth nerve leaves the valve of Vieussens, it forms upon it a conspicuous spinal ganglion of the same character as those on the rootlets of the IIIrd nerve, the cells of which are all degenerated, and the degenerated posterior root fibres are conspicuous between the brain and this ganglion, but cease peripheralwards of the ganglion.

In the VIth nerve the small-fibred part of the anterior root is much more doubtful than in the case of the two preceding nerves; so, too, with the posterior root, its ganglion is limited to a few degenerated nerve cells, and is nothing like so conspicuous as in the case of the IIIrd and IVth nerves.

In the so-called motor root of the Vth nerve we see again distinct groups of small fibres together with the large motor fibres. I have not yet had time to trace out these small fibres to their respective motor ganglia, but have little doubt that they will be found to bear the same relation to the spheno-palatine ganglion as those of the IIIrd nerve do to the oculo-motor ganglion. In the so-called motor root of the Vth nerve is found also a degenerated posterior root, with its ganglion in the same situation and of the same character as in the preceding nerves.

The so-called motor root of the Vth nerve is therefore a complete nerve belonging to the same group as the IIIrd, IVth, and VIth, and does not require the sensory portion of the Vth to make it resemble a spinal nerve.

Leaving aside for the moment the consideration of the sensory part of the Vth nerve we come to the VIIth nerve; here we find the anterior root manifestly composed of a large-fibred and a small-fibred portion, the latter being derived mainly from the *n. intermedius*, though some of the fibres are in the roots of the facial itself. The ganglion geniculatum bears the same relation to these small fibres as the ganglion oculo-motorii to those of the IIIrd nerve, and ganglia which are still further vagrant are seen in the submaxillary ganglion, &c. The ganglion of its posterior root is found in the rootlets of the facial in the usual position, directly after their exit from the brain, and in man both nerve fibres and nerve cells are degenerated in the same way as in the case of the cranial nerves already considered.

The cranial nerves considered up to this point form a natural group all arranged on the same plan with a ganglionated and non-ganglionated anterior root, and a phylogenetically degenerated posterior root and ganglion.

Passing now to the nerves of the medulla oblongata, we find another group with different characteristics. Here there is no sign of any degenerated posterior roots or spinal ganglion; here we find not degeneration of any component but separation of the component parts of a spinal nerve, so that the separate nerves no longer, as in the previous cases, represent each a perfect nerve. Thus in the IXth, Xth, XIth, and XIIth nerves of *man* at all events, the somatic portions of the posterior roots are absent in the nerves themselves with the exception of the auricular branch of the vagus, but clearly are not absent in reality, for the structure of the medulla oblongata shows that they have become diverted from these nerves to help form the sensory part of the Vth, and the Gasserian ganglion. The somatic motor part of this group is present, not as forming a part of each nerve, but as a separate nerve, the hypoglossal or XIIth nerve, the nucleus of origin of which extends along the whole length of the medulla oblongata. The ganglia jugularia of the IXth and Xth nerves which give origin in the Sauropsida to the laryngo-pharyngeal nerve, are the spinal ganglia of the splanchnic portions of the posterior roots of this group, while the ganglion petrosum of IX, and the ganglion trunci vagi (the vagrant character of which is well shown in such animals as the crocodile) are the motor ganglia of the small-fibred portions of the anterior roots of these nerves. Finally, the non-ganglionated splanchnic large-fibred motor nerves have not separated off to form a separate nerve like the XIIth, but remain as

the motor nerves of the laryngeal and pharyngeal muscles. In fact, the IXth and Xth nerves with the medullary part of XI contain all the splanchnic elements belonging to a spinal nerve, or rather a group of spinal nerves, and in man at all events contain none of the somatic elements (with the exception of the auricular branch of the vagus), the somatic portions being represented by the hypoglossal, and a portion of the sensory root of the trigeminal.

Turning our attention to the sensory root of V, we see no sign of any degenerated ganglion or degenerated posterior root; it clearly possesses a functional, well-developed spinal ganglion, the Gasserian; and according to human anatomists, it is exclusively derived from the ascending root of the Vth nerve, *i.e.*, it arises in close connexion with the posterior horn along the whole length of the central nervous system comprised between its point of exit and the middle of the cervical region of the cord. In the absence, then, of any signs of degeneration among its fibres, combined with the presence of a degenerated posterior root ganglion in the so-called motor root of V, we may, I think, fairly conclude from the peculiarity of its origin that the sensory part of V and the Gasserian ganglion does not represent the posterior root of a nerve of which the so-called motor part of V is the anterior root. The explanation of the peculiarities of the origin of the sensory somatic elements of the ascending root of V, as well as of the corresponding sensory splanchnic elements of the ascending root of X must be sought for in the explanation of the presence of the degenerated posterior root ganglia of the Group I of cranial nerves already mentioned.

As far as VIII is concerned, it will suffice at present to say that it does not possess an undoubted degenerated ganglion, that part of it, at all events, possesses a functional spinal ganglion, and that it is a complex nerve, the structure of which requires a much more extensive investigation than I have as yet been able to give it.

In connexion with the presence of these degenerated posterior roots and spinal ganglia, it is significant that in the region of the brain from which these roots spring, groups of strongly pigmented cells are found, the reason for the presence of which is unknown. Of these groups the cells of the *locus cœruleus* are in structure and position clearly the termination of Clarke's column, and are therefore in all probability connected with the remnants of the small-fibred ganglionated efferent portions of some of the nerves of this group; the cells, on the other hand, of the *Substantia nigra* are in apparent connexion with and are embedded in the direct continuation of the degenerated posterior root fibres of the IIIrd nerve.

To sum up, then, it is clear that apart from I, II, and VIII, the rest of the cranial nerves are built up on the same type as the spinal nerves, and that their peculiarities are such as to divide them into

two groups, viz., (1) those which arise from the mid-brain and hind-brain, *i.e.*, III, IV, V_m, VI, VII, all of which are at present, *i.e.*, in man, motor, but possess a degenerated posterior root and ganglion; and (2) those which arise from the med. oblongata, viz., IX, X (in part), XI (in part), XII, V_s (in part), which are characterised not by the loss of any component part, but by the scattering of the different components; a scattering which bears an intimate connexion with the making good of the loss of the sensory elements of Group I.

Finally, certain points connected with the question of the segmental value of the cranial nerves other than those already discussed are worthy of mention. The question of the segmental arrangement of any nerves may as far as their distribution is concerned be considered in a twofold light; 1st, the evidence for any segmental arrangement of somatic parts, as, for instance, of somatic muscles; and 2nd, evidence for any segmental arrangement of splanchnic parts, such as visceral clefts and arches, and the visceral muscles formed from the walls of such clefts.

In order to compare cranial nerves with spinal nerves we must compare structures of the same kind; if the segmental arrangement is based in the one case on the formation of myotomes, then we must search for the corresponding myotomes in the other, if on visceral arches, then we must argue upon the basis of visceral arch formation throughout. Now, van Wijhe has pointed out that the cranial muscles are derived from two groups of muscle segments, (1) a set of myotomes corresponding to the segmented muscle plates throughout the animal which form the muscles I have called non-ganglionated somatic, and (2) a set of lateral plates of mesoblast, lining the walls of the different visceral and branchial cavities, which give rise to the group of muscles which I have called non-ganglionated splanchnic. These latter muscles are unknown segmentally except in the head, they probably form in the trunk, as will be shown immediately, the diaphragm and transversus abdominis muscles.

Now van Wijhe, on the strength of his embryological researches, divides the head of the Selachians into nine segments, with the following arrangement of muscles and nerve supply.

	Muscles from myotomes (somatic).	Visceral clefts.	Muscles from lateral plates (splanchnic).	
1st segment..	Eye muscles, IIIrd nerve			
2nd „ ..	„ IVth „	1. Mandibul.	Vth motor part	
3rd „ ..	„ VIth „	2. Hyoid	VII	
4th „ ..	......			
5th „ ..	......	3. 1st branch.	IX	Mastication and gill muscles.
6th „ ..	......	4. 2nd „	X	
7th „	Muscles from skull to	5. 3rd „	X	
8th „	shoulder girdle XIIth	6. 4th „	X	
9th „	nerve	7	X	

From which we see that if we look upon the myotomes as representing the primitive segmentation, while the visceral clefts and muscles from the lateral plates of mesoblast represent the secondary segmentation (Branchiomery), the 4th, 5th, and 6th segments are unrepresented by any muscles, or rather the 4th and 5th, for he notices the slight muscle formation in the 6th somite, but was unable to trace any special muscle to it.

Now looking at these two groups of muscles, the splanchnic and somatic, we see that the muscles of mastication and expression differ in structure, colour, nature of contraction, and general appearance from the muscles of the eye and the somatic muscles generally, with the exception of the specialised tongue muscles. I find also that the motor nerves of the IIIrd, IVth, and VIth nerves are in the dog much larger in calibre than those of the facial and slightly larger than those of the trigeminal, the eye muscles being innervated by nerves of the same size as the large motor nerves of anterior roots, *i.e.*, from 14·4 μ—18 μ, while the facial muscles are innervated by nerves of the same size as the large motor nerves of the vagus and glosso-pharyngeal which supply the pharyngeal and laryngeal muscles, *i.e.*, from 9 μ—10·8 μ.

Any nerve fibres, therefore, of the size of those of the VIth nerve, for instance, would be very conspicuous and easily followed if they appeared in among the smaller fibres of the facial. Such is the case; the facial roots possess a group of large fibres of the size of the somatic motor nerves in among the smaller fibres; a series of sections through the facial has enabled me to trace one group of these large fibres, and it is a beautiful sight to see them separating out one by one to come to the edge of the nerve, and finally to form a small nerve, which is found to be the *n. stapedius.* The rest of them leave the facial nearer its exit from the brain, and I think pass out as the nerve supplying the *Levator veli palati* muscle. The difficulty, however, of combining the dissection of these parts with the necessary

freshness and freedom from damage which is requisite to ensure a good osmic preparation, has prevented me up to the present from making sure of this latter point.

When the facial leaves the stylo-mastoid foramen it is free from these large fibres. I venture to suggest that the structure of these two muscles, their origins, their shape, colour, and appearance, combined with the size of their motor fibres, all lead to the conclusion that they belong to the same group as the somatic eye muscles, and represent van Wijhe's missing 4th and 5th myotomes. Further, we see this, that if the splanchnic voluntary muscles derived from the lateral plates of mesoblast are differentiated from the somatic voluntary muscles derived from the myotomes by the size of their motor nerve fibres, we ought to find the same relation in the trunk as in the head; this seems to me to be the case, the nerve fibres of the phrenic in the rabbit separate out from those of the 4th and 5th cervical nerves as a group of fibres of smaller size than the surrounding motor nerves of those segments, and also the fibres of the nerve supplying the *m. transversus abdominis* in the dog are distinctly smaller than those of the nerve supplying the *m. obliq. sup.* I conclude then that the primitive segmentation of the head is shown by the somatic muscles of the IIIrd, IVth, and VIth nerves, *m. stapedius*, *m. levator veli palati*, and the muscles of the XIIth nerve, a segmentation which is in agreement with the segmentation of the trunk. In addition to this a secondary segmentation has taken place in the formation of the gills; the muscles belonging to this segmentation show a segmental arrangement in connexion with the gills but not in the case of the trunk, for as far as I know the *m. transversus* and the diaphragm show no sign of segmentation.

In this preliminary communication I cannot discuss all the problems which are opened out by the new light which examination of the structure of the cranial nerves has shed upon their distribution and past history. The explanation of the degenerated posterior roots of certain of the cranial nerves is certainly to be found in the history of the vertebrate animal, and I hope in the course of the summer to publish the full paper of which this is a preliminary account, and in that paper to make some attempt to account for this remarkable phylogenetic degeneration. In conclusion, I may remark that Marshall has previously noticed in the chick a group of ganglion cells at the origin of the IIIrd nerve out of the brain. Also it has been pointed out to me that my discovery of degenerated nerve cells and nerve tissue in such cranial nerves as the IIIrd is not, as I thought, entirely new. The structures in question have been observed by Thomsen and other pathologists. The explanation which I have given is, however, entirely new.